

Species pools and differential performance generate variation in leaf nutrients between native and exotic species in succession

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Abstract

1. A central aim of invasion biology has been to identify key functional differences between native and exotic species to determine which traits may be responsible for invasion success and impacts. There are two primary ways that differences may exist between native and exotic species—the traits of the local species pools may differ, or the way that the traits interact with their environment may differ.
2. We explored leaf nutrient concentrations as functional traits that directly link to plant metabolic processes by sampling healthy, mature leaves from 119 native and exotic taxa across a wide range of successional statuses in New Jersey, USA. Leaf nutrient concentration data (carbon, calcium, magnesium, nitrogen, phosphorus, potassium) were paired with long-term community dynamics from the Buell–Small Succession Study to evaluate abundance-weighted trait values over succession for native and exotic species.
3. After accounting for differences across growth forms, there were minimal differences in foliar nutrients based on plant origin, with only lower leaf carbon and higher leaf potassium in exotic species. However, these differences were not sufficient to generate overall differences between native and exotic species in a multivariate analysis. In contrast, the successional trajectories of the abundance-weighted trait values for most leaf nutrients differed strongly between native and exotic plants. While this pattern may be partially attributable to variation in the species pool for carbon and potassium, successional processes generated differential sorting, suggesting underlying differences in how the same traits function in native and exotic assemblages.
4. *Synthesis.* These results suggest that both variation in the species pool and variation in the successional selection of plant traits can generate functional differences between native and exotic plants. Assessments of trait differences between native and exotic species will require information on traits and plant performance to unambiguously link traits to function in dynamic plant communities.

KEYWORDS

Buell–Small Succession Study, differential performance, functional traits, leaf nutrient concentrations, long-term data, species invasion, succession

1 | INTRODUCTION

One of the major innovations in community ecology has been a shift towards a focus on functional ecology, where suites of traits rather than species' taxonomic identities are used to describe relationships between organisms at the community and ecosystem levels (Duarte, Sand-Jensen, Nielsen, Enríquez, & Agustí, 1995; Keddy, 1992; McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007). Often, a set of core functional traits (e.g., canopy height, seed mass, specific leaf area, woodiness) are used to capture how plants acquire and use resources (Diaz et al., 2004; Weiher et al., 1999; Westoby, 1998). Traits correspond to environmental conditions in which a given group of plants grows and are common across species, making traits more universally descriptive of plant distributions than taxonomic affinity (Keddy, 1992; McGill et al., 2006). As such, plant functional traits have been useful in addressing critical ecological processes such as succession (Douma, Haan, Aerts, Witte, & Bodegom, 2012; Fukami, Martijn, Mortimer, & Putten, 2005; Garnier et al., 2004; Meiners, Cadotte, Fridley, Pickett, & Walker, 2015; Wright et al., 2004) and invasion (Jo, Fridley, & Frank, 2016; Scharfy, Funk, Olde Venterink, & Güsewell, 2011; Tecco, Diaz, Cabido, & Urcelay, 2010; van Kleunen, Weber, & Fischer, 2010).

As functional traits, leaf nutrient concentrations reflect both the physical and physiological function of leaves and thereby may help to explain plant assemblage dynamics. Leaf nutrients are related to plant growth form across a wide range of habitats (e.g., Bigelow, 1993; Foulds, 1993; Thompson, Parkinson, Band, & Spencer, 1997; Han, Fang, Guo, & Zhang, 2005; Bombonato, Siffi, & Gerdol, 2010). Generally, leaves of herbaceous plants tend to have higher levels of macronutrients than woody plants (Bombonato et al., 2010; Foulds, 1993; Han et al., 2005). To understand the mechanisms of plant invasion, some studies have found that exotic plants have higher leaf concentrations of some elements than native plants and have related this difference to their resource acquisition strategies (Foulds, 1993; Jo, Fridley, & Frank, 2015; Osman & Sikder, 2000), whereas others have found no fundamental differences in strategies (Leishman, Haslehurst, Ares, & Baruch, 2007; Leishman, Thomson, & Cooke, 2010; Thompson, Hodgson, & Rich, 1995). Although methodological and conceptual challenges remain (Hulme & Bernard-Verdier, 2018), examining functional differences between native and exotic plants remains a key theme in invasion biology (Dawson, Burslem, & Hulme, 2011; Funk, Cleland, Suding, & Zavaleta, 2008; Leishman et al., 2010; Sutherland, 2004).

Globally, exotic species are often associated with successional or disturbed ecosystems (Bastl, Kocýr, Prach, Pyšek, & Brock, 1997; Meiners, Pickett, & Cadenasso, 2002; Rejmánek & Drake, 1989). We may, therefore, expect the traits of exotics to reflect this association, favouring more resource-acquisitive traits than natives. As successional recovery from disturbance typically involves changes in the dominant life-forms of a plant community, we might also expect leaf nutrient concentrations to vary with the successional status of a species (Bazzaz, 1979; Odum, 1969). Similarly, within a life-form, different physiological strategies might dominate at different positions along a successional gradient (Bazzaz, 1996; Prach, Pyšek, & Smilauer, 1997; Řehouňková & Prach, 2010).

		Species pool	
		Same	Different
Differential performance	Same	Native and non-native species equivalent	Offset trait values but similar successional trajectories
	Different	Divergent selection from equivalent trait pools	Offset trait values and divergent successional trajectories

FIGURE 1 Specification of how the traits of native and exotic plant species can differ during community dynamics. Native and exotic assemblages may differ in the trait composition of the local species pool, or they may differ in how differential performance selects species from the pool that become dominant in the community. By setting the range of traits to select upon, the trait composition of the species pool may, therefore, constrain the trait dynamics generated by differential performance

Plant succession can be conceptualized as a series of differentials, where within a given system, differential performance determines which of the available plant species come to dominate the community over time (Pickett, Collins, & Armesto, 1987; Pickett, Meiners, & Cadenasso, 2011). From this perspective, there are two primary ways that differences may exist between native and exotic species (Figure 1). The traits of the native and exotic species pools may differ and/or the way that traits determine abundance during succession may differ between native and exotic taxa. While the traits of native and exotic are often compared (a species pool effect), how traits assort during community dynamics (differential performance) is rarely examined and represents a critical aspect in understanding the functioning of traits in communities. Mechanistically, these two separate, yet simultaneous, effects shape native and exotic plant communities over successional time.

To fully understand the functional linkages of leaf nutrient concentrations in dynamic plant communities, broad-scale surveys of leaf nutrients linked with long-term community dynamics data are necessary. This study combined a dataset of leaf nutrient composition in 119 plant taxa with a unique long-term succession study to address the fundamental sources of trait variation in the native and exotic plant assemblages. First, we addressed whether leaf nutrient concentrations varied with plant growth form or species origin to assess variation at the level of the local species pool. Second, we examined abundance-weighted trait values over successional time to assess whether variation in the differential performance generated trait differences between native and exotic assemblages.

2 | MATERIALS AND METHODS

2.1 | Study site

The Buell–Small Succession Study (BSS) is a long-term research project documenting successional vegetation changes from abandoned

agricultural fields to deciduous forest. The BSS fields are located in what is now the Hutcheson Memorial Forest Center (HMFC) in the Piedmont region of Somerset County, New Jersey (40°30' N, 74°34' W). Climatic conditions are mesic continental. Mean annual temperature is 11.5°C, ranging from an average high of -1.2°C in January to 23.7°C in July. Mean annual precipitation is 1,180 mm, ranging from 76 mm in February to 123 mm in July (New Jersey State Climatologist; National Climate Data Center). Soils of HMFC are uniform and are derived from Triassic red shale of the Brunswick Formation (Kümmel, 1940; Ugolini, 1964).

The HMFC is a mosaic of deciduous old-growth forest, young forests, and successional fields. The old-growth forest of the site is a mixed *Quercus*–*Carya* canopy (Davison & Forman, 1982; Monk, 1961). This forest is surrounded by the fields of the BSS as well as other areas in various successional stages, including agricultural land. This landscape is thus a heterogeneous mixture of communities representing all successional stages within a small area.

The BSS contains 10 hay and row crop fields, 0.5–1 hectare each, that were abandoned in pairs following either crop harvest (intact litter) or one final ploughing (bare soil) from 1958 to 1964 (Meiners, Pickett, & Cadenasso, 2015; Myster & Pickett, 1990). Vegetation dynamics in each of these fields has been monitored with no subsequent intervention in a series of 48 permanent, 1 m² plots. Plots were censused annually from 1958 to 1979 and biennially thereafter, recording per cent cover of all species growing in each plot. Over time, exotic species in this system have maintained their absolute abundance, despite large-scale transitions in the abundance of life-forms (Figure S1). However, exotic species have proportionately decreased over time as succession has led to an increase in the absolute abundance of natives.

2.2 | Sampling and plant trait analysis

Leaf tissues were collected from 119 taxa across the HMFC in late July over a 3-year period, with most (84%) specimens gathered in 2010. Samples represented 48 families and 94 genera, and included 75 native and 44 exotic species (Duffin, Li, & Meiners, 2018). Species collected were chosen to represent successional dominants throughout the BSS, species characteristic of mature forests, and species currently expanding at HMFC. This selection of species represented 91.4% of the total plant cover included in the BSS data. Gleason and Cronquist (1991) was used to classify species into native/exotic categories and life-forms (forbs, graminoids, woody). Nomenclature follows the USDA NRCS PLANTS Database (<https://plants.usda.gov>) as of June 2014.

Performance of the selected forbs and woody species were relatively equivalent in the BSS (average maximum cover for native forbs = 4.24%, exotic forbs = 4.83%; native woody = 7.41%, exotic woody = 8.68%), but native graminoids were less represented than their exotic counterparts (average maximum cover for native graminoid = 0.90%, exotic graminoid = 11.54%). The abundance of exotic grasses reflects the planting of exotic forage grasses in four of the BSS fields and the colonization of the invasive *Microstegium*

vimineum late in succession. Overall, similarity of peak cover between native and exotic species ensured that we were comparing roughly equivalent pools of successful species.

Leaf samples were taken from healthy mature individuals growing under optimal light conditions to provide a measure of nutrient concentrations when the species would have been at their successional peak. When available, leaves from 10 or more plants were pooled to give a single species value. For small herbaceous plants, several leaves were often taken from 20 or more individuals to collect sufficient tissue for chemical analyses. Equivalent numbers of leaves were taken from each individual regardless of the sample size to ensure equal representation in the final sample. While intraspecific variation can be incredibly important in the trait ecology of communities (e.g., Siefert et al., 2015; Violle et al., 2012), the small size of many of the species explored here precluded addressing that aspect of the system. Leaves were dried at 60°C for 48 hr and stored dry until processed. Samples were sent to the University of Georgia Stable Isotope Lab to analyse leaf nutrient levels. C and N were analysed using Micro-Dumas combustion. P concentrations were obtained through continuous flow colorimetric analysis. Flame atomic absorption spectrophotometry was used to analyse leaf K, Ca, and Mg.

2.3 | Statistical analyses

Analyses revolved around identifying species pool and differential performance-based variation between native and exotic species in succession. To understand the relationships between leaf nutrient concentrations with plant form and origin in the species pool, nutrient data were analysed by growth form (forb, graminoid, woody) and origin (native, exotic), with interaction effects in a two-way MANOVA followed by univariate ANOVAs for each nutrient individually. Univariate ANOVAs were followed with Tukey's HSD post hoc tests to detect differences among growth forms. Nutrient data were log-transformed prior to statistical analyses. To visualize multivariate relationships within the data, principal components analysis (PCA) was conducted on all leaf nutrients across species using a correlation matrix. PCA coordinates from the first two axes were plotted to show form and origin effects.

To account for potential phylogenetic nonindependence among species, we used the phylogeny of BSS species from Li et al (2015) to perform phylogenetic generalized least squares (PGLS) analysis with a variance–covariance matrix of the data based on that phylogeny. Similar to the univariate ANOVAs above, we tested the effects of growth form and origin (and their interaction) on each nutrient individually in the PGLS model. These statistical tests were performed in the R packages *APE* (Paradis, Claude, & Strimmer, 2004), *CAPER* (Orme et al., 2013), *NLME* (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2014), and *PHYTOOLS* (Revell, 2012). The one fern in the dataset, *Asplenium platyneuron*, was removed for this analysis for lack of phylogenetic information. Deleting this species from the phylogenetically uncorrected univariate analyses had no effect on the results presented here. We also used Blomberg's *K* statistic (Blomberg,

Garland, & Ives, 2003) and Pagel's λ statistic (Pagel, 1999) to quantify the phylogenetic signal of the leaf nutrients. The significance of the phylogenetic signals was determined by comparing the observed K and λ values with a null distribution that simulates random trait datasets on the phylogeny for 999 times.

To assess whether the successional trajectories of leaf nutrient concentrations differed between native and exotic species, we calculated abundance-weighted trait values for each leaf nutrient. To do this, the trait value of each species was scaled by the species' relative abundance (based on cover in the BSS data) in each field and year. All species without leaf nutrient data were excluded from this analysis. Abundance-weighted trait values were calculated separately for the native and exotic assemblages to explore their successional dynamics. Abundance values were interpolated between sample years once sampling switched to alternate years. Repeated-measures ANOVA was then run on data from years 1, 5, 10, 15, 20, 25, 30, 35, 40, 45, and 49, the oldest age which all fields had attained. Statistical analyses were conducted using SAS version 9.3 (SAS Institute Inc.) and R 3.3.2 (R Foundation for Statistical Computing, www.R-project.org).

3 | RESULTS

The primary driver of variation in individual leaf nutrient concentrations in the BSS plant trait pool was life-form, which significantly varied in all six leaf nutrients tested (Table 1). Woody species exhibited the expected more conservative nutrient strategy with a higher abundance of leaf C than forbs (Figure 2). Forbs tended to have greater amounts of leaf macronutrients than woody species, although forbs and woody species had statistically similar levels of Ca. Graminoid species varied systematically from both woody and forbs, with intermediate levels of C and N, higher P and K like forbs, and lower Mg like woody species. Graminoids had the lowest Ca levels of all growth forms. While the MANOVA showed no overall effect of species origin on leaf nutrient concentrations once life-form was accounted for, univariate ANOVAs found leaf C was significantly

TABLE 1 Nutrient associations with plant growth form, species origin, and the interaction between form and origin using MANOVA, followed by individual univariate ANOVAs for each nutrient. Significant values are indicated by asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

	Form	Origin	Form \times Origin
Multivariate test	10.61***	1.58	1.70
Univariate tests			
C	15.57***	5.83*	0.28
N	5.73**	1.39	0.29
P	17.47***	0.30	1.96
K	35.15***	6.00*	1.33
Ca	24.02***	0.74	0.18
Mg	9.22***	1.50	0.42

lower and leaf K significantly higher in exotic species across all life-forms (Table 1). Based on Bloomberg's K , there were strong phylogenetic signals in all leaf nutrient concentrations except Mg (Table S1). When phylogeny was accounted for, the significance of origin in leaf K disappeared, although the effect remained for C (Table S2). As phylogeny is related to life-form, including phylogenetic information reduced the importance of life-form to leaf nutrient concentrations, with only C, P, and K remaining significant.

Principal components analysis of leaf nutrient concentrations generated two informative axes explaining 52% and 22% of the variation in the data respectively (Figure 3a). Overall, the distribution of native and exotic species showed a broad overlap within the ordination. There were relatively few outliers in the ordination and these species would have had limited impacts on the dynamics of the system. The exotic forb, *Portulaca oleracea*, (outlier on the far right of PCA I) is a succulent annual that peaked in year 1 after abandonment at 0.63% cover on average. Two grasses were outliers on the negative end of PCA II. The native grass was *Danthonia spicata*, a species with episodic variation in abundance in the BSS, reached a peak cover at year 35 of 1.7%. *Elymus repens* was the exotic grass outlier, and the most abundant, with established populations in the former hay fields of the BSS which spread into the surrounding fields after abandonment. This species had a peak cover of 11.2% in year 5, but this cover collapsed within 10 years.

The mineral nutrients N, P, K, and Mg loaded positively and C negatively with axis I of the PCA (Figure 3b). Axis II was positively correlated with Ca and Mg and to a lesser degree negatively correlated with P and K. Graminoid and woody species tended to load negatively towards leaf C on axis I, while forb species loaded positively towards the metabolic nutrients. PCA axis II separated growth forms cleanly with graminoid species loading negatively, forb species around the origin, and woody species loading positively. There were significant correlations between leaf nutrient composition in the PCA and when a species peaked in succession (year of greatest cover; PCA axis I: $r = -0.203$, $p = 0.0251$; PCA axis II: $r = 0.256$, $p = 0.0046$).

Leaf nutrient patterns by origin were much less striking, reflecting the MANOVA results. Native species loaded slightly more negatively on PCA axis I than exotic species for all growth forms, following the shift in leaf C indicated in the univariate analyses. In contrast, native and exotic species within all growth forms loaded similarly on axis II (Figure 3b). Perhaps due to the smaller size of the species pool, graminoid species had the most overlap between native and exotic taxa on PCA axis I of all growth forms.

In sharp contrast to the analyses of the species pool data, when trait values were weighted by species abundance, clear differences between the trait patterns of native and exotic species appeared during succession (Figure 4 and Table 2). All leaf nutrients other than Mg showed significant patterns over successional time and had either a significant effect of species origin (C, N, P, Ca) or a time \times origin interaction (C, P, K, Ca). Over succession, abundance-weighted trait values generally shifted from high metabolic macronutrient concentrations towards greater leaf C. Following the differences seen within the species pool, the exotic assemblage was consistently

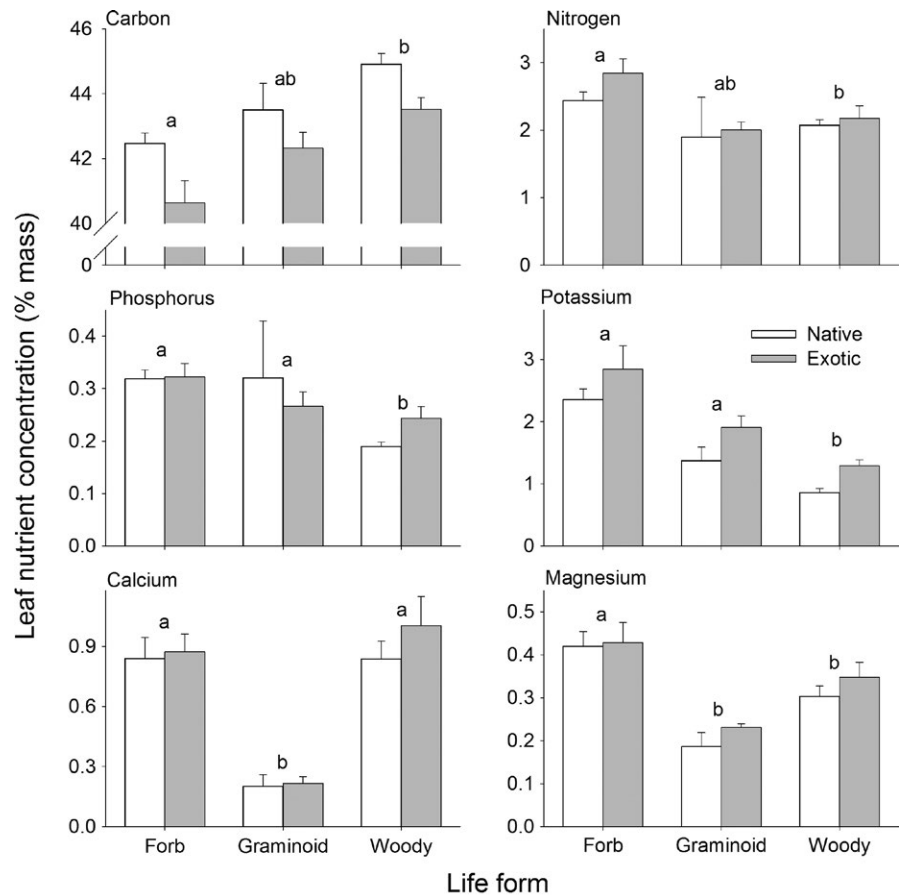


FIGURE 2 Leaf nutrients by growth form and origin. Bars represent $M \pm SE$. Dissimilar letters represent significant difference between growth forms. Note varying scales on y-axes between nutrients

lower in C although the assemblages converged somewhat in the middle during the transition from herbaceous to woody dominated communities. While the pool of exotic species possessed higher K, this shift was only evident in the community early in succession, with natives and exotics converging by year 20. Despite equivalence at the species pool level, exotic assemblages had consistently higher N during succession, although largely similar successional trajectories over time. The remaining leaf nutrients were also equivalent in the species pool, but had markedly different trajectories early in succession. Leaf P and Ca (other than the first few years) of native and exotic assemblages started succession at very similar concentrations, but diverged (higher P, lower Ca in exotics) after year 30.

Although examining life-forms individually removes much of the trait signal in succession, there are still important functional changes that occur (Figure S2). In particular, large changes occur late in succession, as both native and exotic forbs increase N content, the K content of exotic graminoids decreases abruptly, and Ca levels diverge for both native and exotic forbs and graminoids.

4 | DISCUSSION

4.1 | Life-form variation in leaf traits

Leaf nutrient levels in plants varied greatly across growth forms and was a primary driver of the temporal patterns of leaf nutrient concentrations during succession. Forbs had the highest levels of

macronutrients relative to leaf C. This pattern fits the fast growth rate and short leaf life span of forbs relative to woody plants (Grime & Hunt, 1975; Reich et al., 1998; Tilman, 1988; Wright et al., 2004). The forb growth strategy requires relatively high nutrient allocation to leaves, especially of N, in order to maximize photosynthesis and, therefore, carbon capture (Chapin, 1980). In this way, forbs are able to produce biomass and establish leaf area more quickly than more resource-conservative woody plants which allocate appreciable carbon and other resources to produce woody stems and roots. This fast growth cycle allows forbs to have the competitive edge over woody species early in succession. The leaf nutrient profile of graminoids was distinct from both the woody plants and forbs within the BSS. Graminoids, with their blade-like leaves, had comparatively higher levels of C, P, and K than forbs, in relation to the other nutrients. Because forb, graminoid, and woody species have differing leaf nutrient concentrations, as shown here and by others (e.g., Bombonato et al., 2010; Han, Fang, Reich, Woodward, & Wang, 2011), growth form must be accounted for when comparing plant functional traits between native and exotic plants to ensure equivalent comparisons (van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer, 2010).

4.2 | Species pool influences on native and exotic traits

Although multivariate analyses found no overall variation in leaf nutrients, native plants had higher C and lower K levels (when not

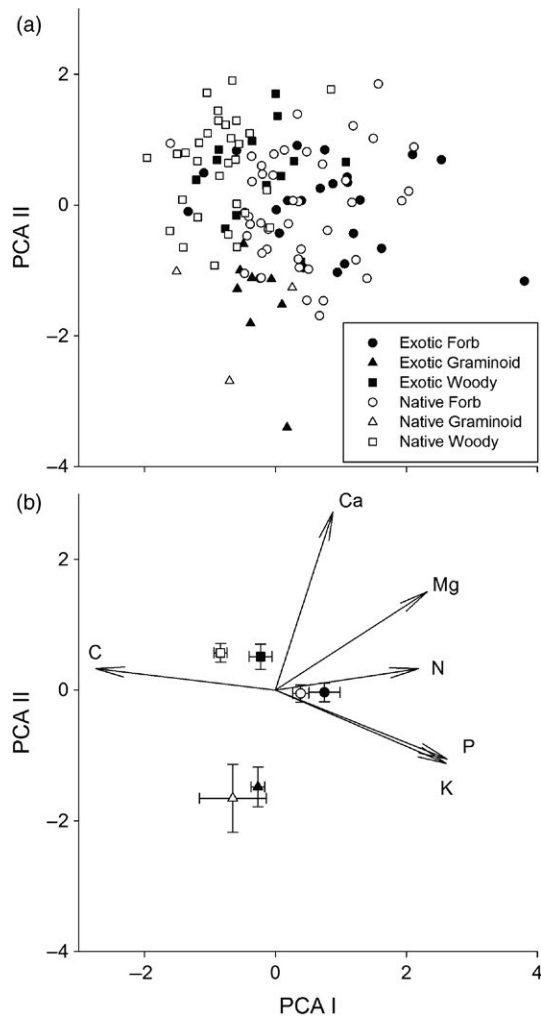


FIGURE 3 (a) Forb ($n = 66$), graminoid ($n = 13$), and woody ($n = 43$) species by origin (native or exotic) as they relate to principal components analysis (PCA) axis I and II. (b) Relationship between leaf nutrients using PCA and average values of growth form by origin as they relate to PCA axis I and II. Values plotted are $M \pm SE$

accounting for phylogenetic relationships) compared with exotic plants in the univariate analyses. Despite having evolved in separate ecological communities, exotic species possess levels of most foliar nutrients similar to equivalent native species in this community. Native and exotic species are often thought to occupy fundamentally different trait space (Leffler, James, Monaco, & Sheley, 2014) explaining the success of nonnative invaders. However, the multivariate distribution of leaf traits showed that both native and exotic species occupied an equivalent range of leaf nutrient niche space. This overall similarity further substantiates the hypothesis that native and exotic species are not functionally different (Leffler et al., 2014; Thompson & Davis, 2011; Thompson et al., 1995). Regardless of origin, particular suites of traits define a successful plant, and these traits tend to reflect the nutrient-rich and disturbed habitats prevalent in modern environments such as those explored here (Dainese & Bragazza, 2012; Kyle & Leishman, 2009; Leishman et al., 2007, 2010; Thompson & Davis, 2011). Overall, similarity in the trait

composition of the species pool here is consistent with the meta-analysis of Kleunen, Weber, et al., 2010, which found differences between invasive and native species disappeared when comparing the traits of invasives to native species that were invasive elsewhere, a situation close to that evaluated here. Ultimately trait differences across species should translate to population dynamics in order to be truly functional. However, native and exotic species within the BSS have similar population dynamics based on frequency and cover metrics (Meiners, 2007; Meiners, Rye, & Klass, 2009) further arguing for the equivalence of the species pool in this system.

Despite the overall trait similarity of the pools of native and exotic species, the individual variation in leaf C and K may have important ecosystem implications. In a variety of systems, exotic plant species have been shown to alter nutrient concentrations and turnover (Ehrenfeld, 2003). For example, despite overall similar rates of decomposition for root and leaf tissues in a suite of woody plants of the northeastern United States, exotic species resulted in a net increase in the rate of N cycling (Jo et al., 2015, 2016; Jo, Fridley, & Frank, 2017). A subset of those species also possessed faster root turnover, which was associated with higher N uptake and faster growth capacity between native and exotic congeners (Smith, Fridley, Goebel, & Bauerle, 2014). Furthermore, selective herbivory on native and exotic species may additionally alter nutrient and energy transfer in invaded ecosystems (Cincotta, Adams, & Holzapfel, 2009; Fortuna et al., 2014).

4.3 | Differential performance generates functional divergence in succession

The temporal patterns in community-weighted leaf nutrient concentrations largely reflected the changes in life-form in succession, and overall represented the expected successional transition from resource acquisitive to resource-conservative strategies. Secondary to the changes associated with life-form, were the differences imposed by the nutrient dynamics of native and exotic species. While differences between the C and K of native and exotic species exhibited by the species pool may be expected to result in functional shifts at the community scale, significant temporal differences were also seen in N, P, and Ca, which did not vary in the species pool.

The temporal dynamics of individual nutrients reveal differing contributions of the species pool and differential performance to successional trajectories. Higher leaf N throughout succession was not a product of exotic species in the pool having higher leaf N, but rather the exotic species that became abundant had higher N than the native species that became abundant. The variation in leaf C through succession, in contrast, could have been entirely generated by the greater leaf C exhibited in the native species pool. Interestingly, C and N, the most commonly studied leaf nutrients, both had roughly consistent differences between exotics and natives throughout succession. However, both N and C had some convergence between native and exotic trajectories in the middle of the successional sequence (a significant time \times origin interaction in C). Although the absolute nutrient differences may have important

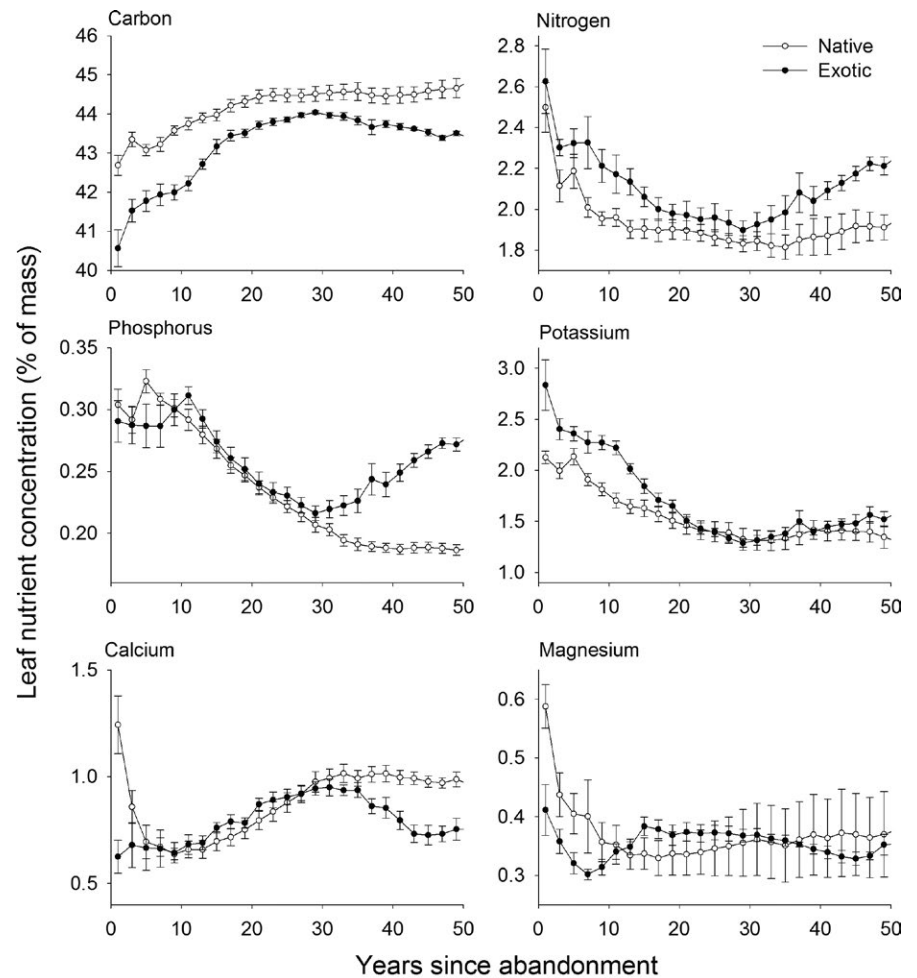


FIGURE 4 Temporal trajectories of leaf nutrient concentrations for native and exotic species. Data plotted are the mean abundance-weighted trait values of the 10 Buell–Small Succession Study fields, with the error bars representing the standard error across fields

consequences for decomposition and nutrient dynamics (Jo et al., 2015, 2017; Mason, Carswell, Richardson, & Burrows, 2010), the similarity of the temporal trajectories suggest the same underlying drivers of functional change in succession (Fukami et al., 2005). The successional trajectories of these two nutrients are consistent with the parallel dynamics hypothesis (Martinez, Gibson, & Middleton, 2015; McLane, Battaglia, Gibson, & Groninger, 2012), where native and exotic plant assemblages exhibit equivalent temporal dynamics. However, the shift in abundance-weighted trait values show that exotic species are displaced towards more resource acquisitive strategies (lower C, Higher N), perhaps representing a fundamental shift in resource allocation (Leishman et al., 2007, 2010).

In marked contrast to the largely parallel dynamics of C and N, the leaf nutrients P, K, and Ca had markedly different leaf nutrient concentrations between native and exotic assemblages for a portion of the successional trajectory, and quite similar concentrations for the remainder. Although there was a consistently higher concentration of K in the leaves of exotic species across all life-forms, this difference only manifested itself over the first 20 years of succession, with nearly identical concentrations in older communities. Leaf P and Ca exhibited the opposite pattern, with equivalent concentrations early in succession, which rapidly diverged late in succession, roughly following canopy closure in most plots. Again, the

equivalence of the native and exotic pools in these nutrients did not translate to successional equivalence as expressed by the community. Variation in the leaf nutrient trajectories of natives and exotics was clearly generated by both differences in species performance (P, K, Ca) as well as variation in the trait pool (K only). Adequate understanding of trait dynamics in community assembly will depend on knowledge of both the pools of traits involved as well as their functional responses over time.

It is tempting to assign the observed functional shifts to the abundance of one dominant invader, but that is not the case in this system. For example, *Alliaria petiolata* is a late successional, invasive forb with high leaf P that has become abundant within the BSS. However, woody exotics such as *Ailanthus altissima* and *Elaeagnus angustifolia* also have high leaf P and are abundant in years 40 and later and contribute heavily to the increase in exotic leaf P late in the successional sequence explored here. Native late successional forbs, such as *Circaea lutetiana*, *Hackelia virginiana*, and *Verbena urticifolia*, also have equivalent or higher leaf P than *A. petiolata*, but have much lower abundances in the system. While the shift towards more acquisitive resource use patterns in dominant exotics appears to be a general phenomenon across this succession, the responsiveness of individual leaf nutrients would likely vary based on site context. As natives with similarly high P levels to exotics are present in the BSS

TABLE 2 Variation in leaf nutrient concentrations of native and exotic species over successional time. Temporal trajectories were generated using trait values weighted by species' abundance in the Buell–Small Succession Study. Within-subject effects report univariate repeated-measures tests using a Greenhouse–Geisser correction. Significant *p* values indicated in bold

Source	<i>df</i>	<i>F</i>	<i>p</i>
Carbon			
Time	10,170	56.12	<0.0001
Origin	1,17	24.64	<0.0001
Time × Origin	20,170	5.21	0.0017
Nitrogen			
Time	10,170	14.68	<0.0001
Origin	1,17	9.41	0.0018
Time × Origin	20,170	1.72	0.1404
Phosphorus			
Time	10,170	18.58	<0.0001
Origin	1,17	9.79	0.0015
Time × Origin	20,170	9.21	<0.0001
Potassium			
Time	10,170	40.59	<0.0001
Origin	1,17	2.84	0.0862
Time × Origin	20,170	2.64	0.0468
Calcium			
Time	10,170	3.45	0.0221
Origin	1,17	5.93	0.0111
Time × Origin	20,170	4.59	0.0007
Magnesium			
Time	10,170	2.00	0.8543
Origin	1,17	0.15	0.1534
Time × Origin	20,170	2.58	0.0582

at low abundances, the observed differences between assemblages may decrease over time if those similar native species increase in the system.

It is important to note that the variation between native and exotic species noted here does not specifically reflect the process of invasion, as the species selection procedure used specifically focused on species successful within the BSS. Rather, these data represent shifts in the ecological strategies of dominant species as the community has assembled from the local pool. As such, changes in leaf nutrient concentrations during succession have important implications for the reciprocal effects of species on soils and nutrient dynamics (Birouste, Kazakou, Blanchard, & Roumet, 2012; Cornwell et al., 2008; Diaz et al., 2004; Lee et al., 2017). The importance of any of these changes on ecosystem processes, including those associated with dominance by exotic species, will be dependent on local limitations and conditions.

There are two primary caveats to this work: species variability and combining life-forms into a single analysis. As leaf nutrient

concentrations may vary with growth conditions (Violle et al., 2012), we may also expect to see plasticity along succession, potentially offsetting some of the dynamics documented here. As the life-forms had more consistent variation, the larger successional signal should have been robust to this limitation. Although succession is inherently a transition in life-forms, an effective way to combine these into a single analysis is difficult. Here, we used measures of abundance based on aerial cover, but the same amount of cover likely reflects different leaf abundances across life-forms. Although trait-based studies often focus on a single functional group, plant communities typically contain multiple life-forms and therefore trait-based analyses must be able to reflect that condition.

5 | CONCLUSIONS

One of the primary arguments against comparing the traits of native and exotic species is the difficulty in determining which traits are ultimately important in determining plant success (Hulme & Bernard-Verdier, 2018; Thompson & Davis, 2011), running the risk of erroneously assigning ecological function to an unimportant difference. In the survey presented here, we found native and exotic species to be functionally equivalent in a multivariate view, and to only differ in leaf C and K when examined individually. In marked contrast, combining trait data with the long-term record of species performance at the site revealed large changes in the successional trajectory of not only those nutrients which differed in the species pool (C, K) but also those which did not (N, P, Ca). Therefore, the lack or presence of differences between the pools of native and exotic species was not particularly useful in understanding the temporal dynamics exhibited by the system. Our results clearly suggest that both variation in the species pool and variation in the successional selection of plant traits generate functional differences between native and exotic plants during succession. Examining differences in trait pools between natives and exotics only captures one aspect of plant invasion. While much more difficult, including clear measures of plant performance are needed to fully understand the impacts of exotic species on ecosystem processes.

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AUTHORS' CONTRIBUTIONS

S.J.M. collected leaf samples, K.I.D., S.L., and S.J.M. conceived the study design, conducted data analyses, and contributed to the manuscript.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j968847> (Duffin, Li, & Meiners, 2018).

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